Amphibians: Lungs' Lift Lost

The reduction or loss of lungs in some amphibian species is a rare evolutionary occurrence. The discovery of the first lungless frog sheds further light on the physiological, morphological and behavioral changes that allowed sufficient external respiration in the absence of lungs.

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Among tetrapods, the loss of lungs is very rare and occurs only in amphibians. In particular, salamanders of the family Plethodontidae (several genera and many species); two species of salamanders (*Onychodactylus,* family Hynobiidae); and one caecilian (Gymnophiona, *Typhlonectes eiselti*). Now, a single species of frog joins this list, as writing in this issue of *Current Biology,* Bickford and colleagues [1] have discovered that the Bornean frog *Barbourula kalmantanensis* (family Discoglossidae), previously known from only two specimens, lacks lungs.

Early in the evolution of amphibians, an inefficient buccal force pump arose whereby air was forced into the lungs against a positive pressure. The pumping action results from a forceful rise of the buccal floor and expiration is mostly passive [2]. These characteristics rendered amphibians particularly susceptible to lung loss, along with increases in the ratio of body surface area to body mass, mechanisms for increased ventilation across the skin and morphological changes that allow penetration of capillaries into the epidermis. The loss of lungs is often associated with low metabolic rates in cool habitats with higher O_2 and lower CO_2 concentrations. These factors are likely to have placed evolutionary constraints on body size and shape as well as habitats that could be exploited [2-4]. Very large-bodied aquatic salamanders (*Andrias, Amphiuma, Cryptobranchus* and *Siren*) evolved mechanisms utilizing highly muscularized lungs that contract forcefully for expiration, thus escaping the problems encountered by other amphibians, although their lungs are inflated during inspiration by the buccal pump [5]. The loss of lungs generally takes place in amphibian species that live in aquatic environments where too much buoyancy can become a problem. The current consensus on the origin of plethodontid salamanders (Figure 1), the largest group of lungless amphibians, is that the loss of lungs took place first in mountain streams of the southern Appalachian Mountains, the center of origin and dispersal of the family Plethodontidae. The lung loss would have prevented animals from being dislodged and swept downstream, but alternative causes have been proposed [6,7]. The newly discovered loss of lungs in the Bornean frog *B. kalimantanensis* seems to support this idea as also this frog appears to be living in cool, fast-flowing streams. The relatively small size and flattened body result in a high surface-area to body-mass ratio that would facilitate respiratory gas exchange through the skin. Also, the metabolic rate would be low in the cool environment, thus less oxygen would be required. By contrast, nothing is known about the habitat of the single

Figure 1. Terrestrial lungless salamanders of the family Plethodontidae.

Bolitoglossa mexicana (upper panel), living in Mexico and Central America. Photo by Dante Fenolio. *Bolitoglossa schizodactyla* (lower panel), northern Colombia and Panama. Photo by Dante Fenolio.

Figure 2. The Titicaca frog.

An adult Lake Titicaca frog (*Conraua goliath)* with extensive skin folds for aquatic respiratory gas exchange at high altitude. These frogs have much reduced lungs and normally do not surface to breath air. Photo by V.H. Hutchison.

lungless caecilian as it is only known from a single museum specimen in the Vienna Museum collected prior to 1920 from an unknown South American habitat [3]. There are currently six recognized families of the widely distributed and tropical caecilians, only one (Typhlonectidae) of which is aquatic. The terrestrial forms are secretive burrowers and resemble snakes or large earthworms.

Instead of a complete loss of lungs, other aquatic amphibians show a reduction in lung size and function, which also is an apparent adaptation to reduce buoyancy. For instance, the large stream-dwelling hellbender salamanders (*Cryptobranchus*) have somewhat reduced lungs and depend upon body-rocking movements and a wrinkly skin surface for much of their gas exchange, while the lung serves primarily as a hydrostatic organ [8]. Lung function is also reduced in the aquatic mudpuppies (*Necturus*), but they retain gills as adults [9]. The strictly aquatic Lake Titicaca frog (Figure 2) (*Telmatobius culeus*) has not been seen in the field to surface for air and occurs at fair depths, but can be forced to ventilate air in the laboratory. The lung is greatly reduced (less than one-third of the lung size of a terrestrial frog of the same size) and respiratory gas exchange occurs across the large skin folds and flaps. The Titicaca frog has a suite of physiological, morphological and behavioral adaptations for an aquatic habitat at high altitude where the partial pressure of atmospheric oxygen is reduced significantly. These adaptations include a low metabolic rate, the smallest erythrocyte volume for any amphibian, very low P_{50} of the oxygen-dissociation curve (which allows the near saturation of hemoglobin at the low partial pressure of oxygen in the environment), the highest erythrocyte count of any frog and elevated blood oxygen capacity, hemoglobin concentration and hematocrit. If placed in water of low oxygen content, they employ a 'bobbing' behavior to ventilate the large skin flaps that act much like 'gills' with high capillary density and capillaries that penetrate the stratum corneum [10].

Lung reduction in amphibians may also occur for reasons other than buoyancy reduction. The semi-aquatic Goliath frog (*Conraua goliath),* the largest known frog (about 300 grams), lives in West African rainforests along streams near waterfalls and rapids. The lung is reduced to about one-third of the volume of other frogs of similar mass and the heart is also smaller. Unlike most frogs in the family Ranidae, goliath frogs are aerobic sit-and-wait predators. They have a reduced metabolic rate and a unique suite of breathing mechanics. And unlike in other frogs, each buccal movement pumps air into the lungs at a rapid rate and the extraction of oxygen from the air is actually slightly better than in other ranids. These adaptations are not associated with buoyancy, but are apparently useful for the production of reproductive and territorial calls in the rather loud white noise of the rushing waterfalls and rapids in the frog's habitat [11]. Normally, small frogs call at high frequencies while large ones call at low frequencies. The call of the goliath frog, however, shows an unexpectedly high frequency of 4.14 kHz, and the frog calls with its mouth open.

The important role of frog calls in advertising territoriality and for reproduction is well known. So, how do frogs without lungs compensate for the lack of a voice? Some species appear to use brightly colored limbs that contrast with environmental surroundings to attract females during courtship. Another Bornean ranid frog, *Staurois parvus*, that lives in waterfall habitats kicks out its hind limbs to display blue webbing of the foot that contrasts with the dull buff and olive color of the other parts of the body [12].

Loss of lungs may occur in other small, stream-dwelling frogs in cool environments. Specimens deposited in museums are not often dissected to check internal organs; a survey of likely candidates may produce additional examples. The reports of other small Asian frogs with bright webbing [12] suggest that they may use visual cues in place of vocal signals. Field observations may also reveal reproductive behaviors that suggest lung reduction or loss. Since nothing is known about the physiological adaptations of *B. kalmantanensis*, laboratory studies would be interesting should sufficient animals be available. However, sound conservation efforts are required to preserve this apparently rare frog.

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